Toyotamaphimeia cf. machikanensis (Crocodylia, Tomistominae) from the Middle Pleistocene of Osaka, Japan, and crocodylian survivorship through the Pliocene-Pleistocene climatic oscillations

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ABSTRACT

Crocodylians are ectothermic animals, and their past distribution has been greatly influenced by changing climate since their Cretaceous origin. The Pliocene-Pleistocene witnessed a contraction of the crocodylian latitudinal ranges due to rapid cooling with superimposed pronounced orbital-scale climate oscillations. However, a chronologically-continuous record of the geographically marginal populations of crocodylians is yet to be provided for this time interval, and crocodylian response to such climatic changes is poorly known. This study describes a partial crocodylian skeleton from the Middle Pleistocene of Osaka, Japan, diagnosed as *Toyotamaphimeia* cf. *machikanensis*, on the basis of character comparisons, including ontogenetic skull shape change, and consideration of the reconstruction error in the holotype of *T. machikanensis*. Pliocene-Pleistocene record of fossil crocodylians in the Kinki, Tokai, and Kanto districts of Japan extends from ~3.5 Ma to ~0.3 Ma. The paleotemperature estimates for the crocodylian-bearing horizons indicate that late Early–Middle Pleistocene crocodylians in the Kinki district of Japan were living near their lower thermal limit. During the glacial periods, they might have moved to the southern extremity of Japan or locally became extinct from Japan, while re-expanding their range after the end of glacial periods.

1. Introduction

Crocodylians rely on an external source of heat, and metabolic heat production minimally contributes to their thermal budget (Seebacher et al., 1999). Although extant crocodylian species can tolerate a wide range of temperatures, they may not survive with the body temperatures below 4–5 °C, which is the critical minimum temperature measured for American alligators (Brisbin et al., 1982). Under freezing air temperatures with ice covering the water surface, large American alligators make small breathing holes around their noses and stay underwater until the air gets warm enough (Brisbin et al., 1982; Hagan et al., 1983; Brandt and Mazzotti, 1990; Grigg and Kirshner, 2015). Meanwhile, the minimum ambient environmental (water) temperature for American alligators is reported as 2–4 °C (Brisbin et al., 1982; Hagan et al., 1983), which is close to the critical minimum body temperature for the same species, suggesting that extremely low environmental temperature limits individual survival. In the long run, prolonged cold temperatures delay and shorten the breeding seasons (Joanen and McNease, 1989), hence hindering reproductive success. Growth rates are also decreased in colder areas due to the longer periods of suppressed appetite, thus northern populations of the American alligator take longer time to reach maturity (Lance, 2003).

As consistent with these observations, temperature as well as the presence of standing water are principal factors determining the distribution of crocodylians (Markwick, 1998a). Modern crocodylians, including 27 + species in nine genera (Grigg and Kirshner, 2015) are mostly restricted to the tropics and subtropics. Their northern and southern distribution limits are ~36°N for *Alligator mississippiensis* in

northeastern North Carolina (Elsey and Woodward, 2010) and ~33–34°S for *Caiman latirostris* in central Argentina and Uruguay (Verdade et al., 2010), while several other species polewardly extend their ranges to 30°N or 30°S (*Alligator sinensis, Caiman yacare, Crocodylus palustris, Crocodylus niloticus*, and *Gavialis gangeticus*: Campos et al., 2010; da Silva and Lenin, 2010; Jiang, 2010; Stevenson and Whitaker, 2010). As expected from extant species, the fossil record suggests that climate, and in particular temperature, contributed to biodiversity and evolution of crocodylomorphs (Markwick, 1998b; Carvalho et al., 2010; Martin et al., 2014; Mannion et al., 2015). For the crown-group crocodylians, it has been known that their latitudinal ranges have been greatly changed since the Cretaceous Period, being much wider in warmer times and narrower in colder times (Berg, 1964). Using a large dataset of fossil crocodylians, Markwick (1998a, 1998b, 2007) showed that during the Cretaceous–Middle Eocene, their distribution was extended to 60°N and higher paleolatitudes, with the most poleward record found in the Early Eocene of Ellesmere Island, Canadian Arctic Archipelago (Estes and Hutchison, 1980). After the appearance of the major ice sheets in the Late Eocene, their latitudinal range has gradually contracted. Through the rapid climatic deterioration over the late Pliocene–Pleistocene, they had been constrained to low latitudes and coastal regions of mid latitudes (Markwick, 1994, 1998a, 1998b, 2007), similar to the Present. Because the late Pliocene–Pleistocene is characterized by the large orbital-scale climate oscillations, a number of studies has examined the effect of such large climate fluctuations on animal and plant biogeography and evolution, using both fossils and DNA (e.g., Hewitt, 2000; Davis and Shaw, 2001; Sommer and Zachos, 2009). However, for Pliocene-Pleistocene crocodylians, a chronologically continuous fossil record of geographically marginal populations in the mid-latitudes is yet to be provided, and the interplay of their distribution and climate patterns is rarely discussed.

The Japanese archipelago is rich in Pliocene-Pleistocene deposits, which are mainly distributed in the coastal areas of the Pacific Ocean and the Japan Sea (Itihara, 1993; Satoguchi and Nagahashi, 2012). Pliocene-Pleistocene crocodylians were abundantly found on the Pacific side of the Honshu Island, as best represented by a nearly complete skeleton of a tomistomine, *Toyotamaphimeia machikanensis* from the Middle Pleistocene Osaka Group (Kobatake et al., 1965; Aoki, 1983; Kobayashi et al., 2006). The Osaka Group, as well as other crocodylian bearing units (Kobiwako, Tokai, and Kazusa Groups) are located at 34–36°N that roughly equals the northern distribution limit of extant crocodylians. These deposits are intercalated by numerous tephra beds, and the local tephras are correlated with each other (Satoguchi and Nagahashi, 2012), thus crocodylian occurrences can be sequentially ordered. Moreover, for many rock units, local climates are reconstructed by using pollen and plant fossil records (e.g., Iwauchi, 1994; Momohara, 1994; Nakagawa et al., 2002), therefore the crocodylian record can be discussed with the regional climate patterns.

In this paper, we describe a well preserved crocodylian from the Middle Pleistocene of Kishiwada City, Osaka Prefecture, which was preliminarily examined and briefly discussed in Taruno (1999) and Kobayashi et al. (2006). We also compile a well-dated fossil record of Japanese Pliocene-Pleistocene crocodylians. In reference to global and local climate data, crocodylian response and survival potential during the Pliocene-Pleistocene climate deterioration are discussed.

2. Materials and methods

2.1. Description and phylogenetic analysis

We describe the osteology of a crocodylian material from the Middle Pleistocene of Osaka, Japan (KSNHM-F7-6) accessioned in the Natural History Museum, Kishiwada City, Osaka, Japan. A phylogenetic analysis was performed by adding KSNHM-F7-6 into Shan et al.'s (2017) taxon-character matrix that is largely based on Jouve et al. (2015), using TNT 1.5-beta (Goloboff et al., 2003). 67 ingroup taxa and 238

characters were employed in the analysis. *Bernissartia fagesii* was used as an outgroup, and a heuristic search was run with 1000 random addition sequence replicates of Wagner trees, and tree bisection reconnection branch swapping. 10 trees per replication were saved. All characters were unordered and equally weighted. Character scorings of the holotype of *Toyotamaphimeia machikanensis* (MOU F00001) and *Penghusuchus pani* (NMNS-005645) were modified based on the direct observation (see Appendix 2).

2.2. Paleotemperature reconstruction

We reconstructed the coldest-month mean temperature (CMMT), warmest-month mean temperature (WMMT), and mean annual temperature (MAT) of the crocodylian-bearing interglacial stages (MIS 35, 31, 17 and 13) in the Kinki district of Japan, based on the climatic requirements of the nearest living relatives of the plant macrofossil (mainly fruit and seed fossils) assemblage components (Mosbrugger and Utescher, 1997; Yamakawa et al., 2017). To reconstruct paleotemperatures at the site of fossil deposition, we selected the most thermophilous and the most cold-loving plants. These plants provide the warmest temperature values among the coldest limit temperatures and the coldest temperature values among the warmest limit temperatures respectively, of the macrofossil assemblage components. Paleotemperatures at the site of fossil deposition are warmer than the coldest temperature limit of the most thermophilous plants, while the warmest limit temperatures of the most cold-loving plants constrains the warmest limit of estimated paleotemperature (Mosbrugger and Utescher, 1997). However, temperature estimates using the cold-loving plants should be interpreted carefully because such taxa could be transported from higher altitudes (Yamakawa et al., 2017). Using the climate databases (IDBMC, 1984; JMA, 2002), we obtained the temperature variables at the selected plant's current northern/southern distribution limit in reference to local floras in which the distribution of taxa is described and/or mapped on an altitudinal scale of at least 100 m based on herbarium specimens and/or field observations.

3. Systematic paleontology

Crocodylia Gmelin, 1789 (*sensu* Benton and Clark, 1988)
Tomistominae Kälin, 1955 (*sensu* Brochu, 2003)
Toyotamaphimeia Aoki, 1983
Toyotamaphimeia cf. *machikanensis* Kamei et Matsumoto in Kobatake et al., 1965

3.1. Material

KSNHM-F7-6, incomplete skull, mandible, tooth, hyoid, humerus, pubis, femur, vertebrae, rib and dorsal osteoderms.

3.2. Institutional abbreviations used in text

GMNH, Gunma Museum of Natural History, Gunma, Japan; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; KSNHM, Natural History Museum, Kishiwada City, Osaka, Japan; LBM, Lake Biwa Museum, Shiga, Japan; MOU, Museum of Osaka University, Osaka, Japan; NMNS, National Museum of Natural Science, Taichung, Taiwan; OMNH, Osaka Museum of Natural History, Osaka, Japan.

3.3. Locality and horizon

A tomistomine fossil was discovered 7.5 m below the pavement at an intersection (N34.440119, E135.389582) in Nagareki-cho, Kishiwada City, Osaka prefecture in 1994, during a sewerage construction. The stratigraphic section of the locality (Fig. 1) shows that the specimen is derived from the sandy silt layer near the bottom of the marine bed 5 (Ma 5) of the Senpoku Formation in the upper part of the
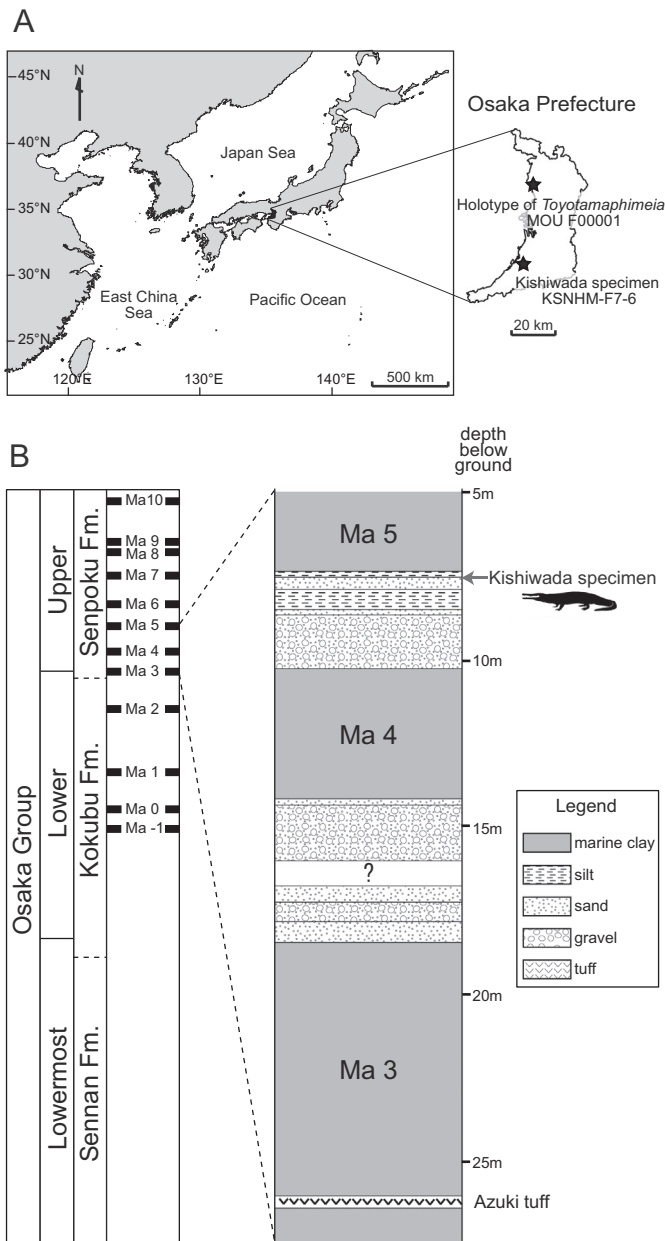
Fig. 1. A, localities of two Japanese tomistomine specimens (MOU F00001 and KSNHM-F7-6). B, stratigraphic column of the locality of the Kishiwada specimen (based on Taruno, 1999; Yoshikawa, 1993). Ma, marine bed in the Osaka Group. A crocodylian silhouette modified from Kobayashi et al. (2006).

Osaka Group (Taruno, 1999). The Osaka Group is the Pliocene and the Pleistocene unit, which is exposed on the hills and terraces in the Osaka Basin. The lower to upper parts of the unit are characterized by cycles of fluvio-lacustrine beds and 12 marine beds intercalated by a number of volcanic ash layers, in which the marine and volcanic ash layers serve as key beds (Itihara, 1993). As to the age of the fossil bearing horizon (Ma 5), Azuki tephra, the volcanic ash layer in the lower part of Ma 3 that is 20 m below Ma 5 was dated at 0.87 ± 0.07 Ma by fission track dating (Nishimura and Sasajima, 1970). Recent correlation of the Osaka Group with the oxygen isotope record showed that Ma 5 was assignable to the marine isotope stage 17 (Masuda and Ito, 1999; Yoshikawa and Mitamura, 1999), which started at 712 ka (Lisiecki and Raymo, 2005).

3.4. Integrity of specimen

Remains can be attributed to a single individual (Taruno, 1999) because (1) most of the post-rostral skull elements were sutured when discovered, (2) all the skeletal elements were found in the small area (vertical shaft of 2.4 m diameter), and (3) all elements are compatible in size without element duplication. Here, cranial elements are described only. Description of hyoid and postcranial elements can be found in the supplementary information (Appendix 1).

3.5. Skull description

In the skull, middle to posterior portion of the rostrum, skull table, infratemporal region, upper portion of the occipital are preserved (Fig. 2).

The maxillae preserve their middle to posterior portion, while the dorsal and palatal parts are separated. The dorsal surface of the maxillae is relatively smooth and is not ornamented with pits or grooves. In the dorsal part of maxillae, several alveoli are recognized. For the left maxilla, the fourth alveolus from the front is the largest. The palatal part of maxillae shows the anterolateral boarder of the suborbital fenestrae (SOF). In the left maxilla, the seventh alveolus anterior to the SOF is surrounded by the slightly elevated ridge, representing the largest maxillary tooth position. Except for this alveolus, the palatal surface of the maxillae is flat and at the same level with alveolar margins. Anterior to the left SOF, the suture for the palatine extends anteromedially. Medial to the third alveolus anterior to the SOF, a large oval shape foramen (11.2 mm long) for the exit of the cranial nerve V is present.

The nasals are rod-like anteriorly. Posteriorly near the level of the maxilla-lacrimal suture, the nasals widen and become sheet-like, and pinch the anterior frontal process.
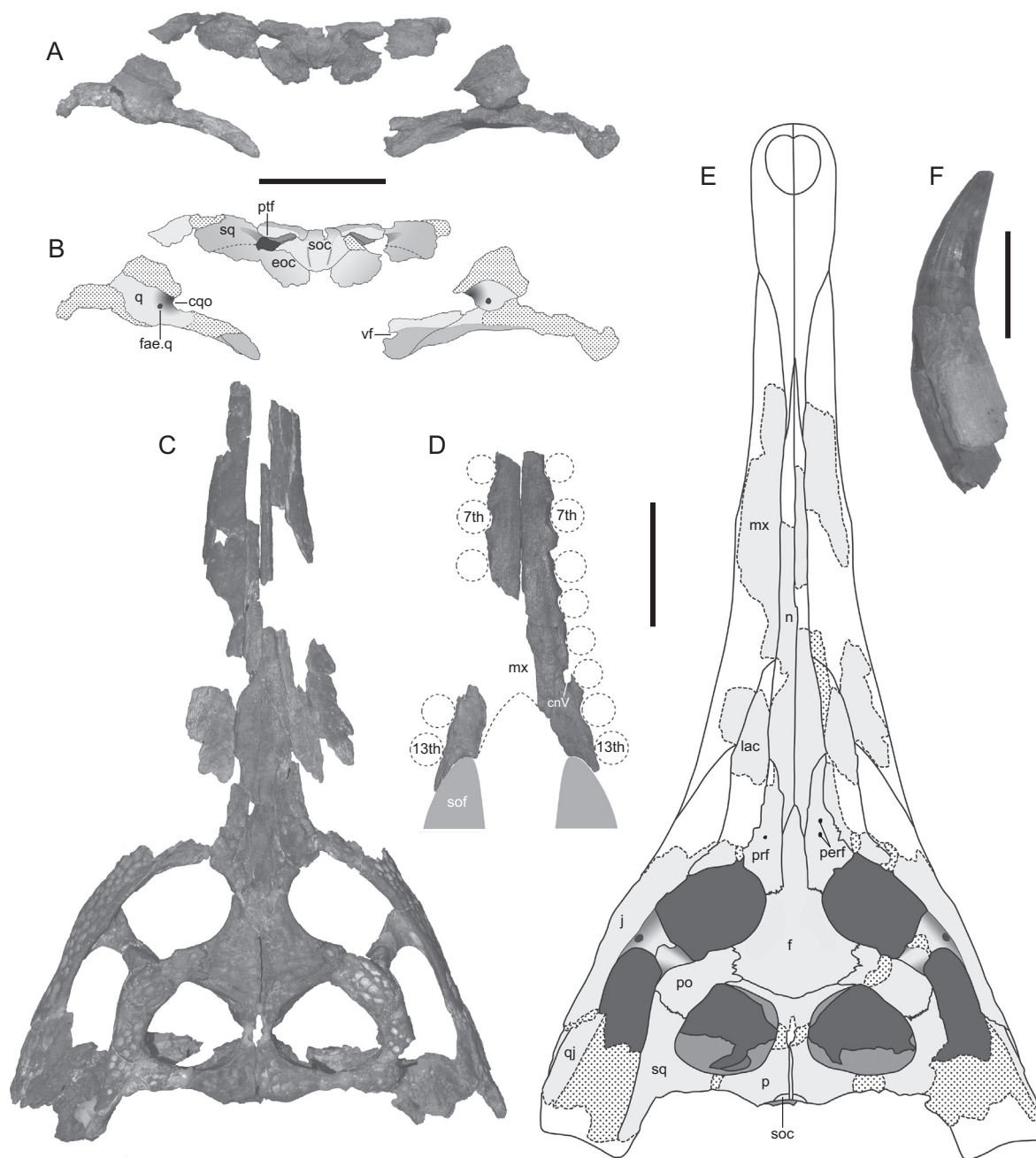
The lacrimals form the anterior margin of the orbits, and extend far more anterior than the prefrontals and frontal, although their anterior extremities are broken.

Each prefrontal forms the anteromedial corner of the orbit. It is widest at the orbital margin, and tapers anteriorly, with its anterior extremity projecting further forward than the frontal. On the dorsal surface, a small perforation is seen in the middle of this element.

The frontal forms the posteromedial corners of the orbits. It is narrow at the contact with the prefrontals, and sends a slender process anteriorly. Although its sutural contact with the nasals are damaged, its anterior tip seems to form a simple acute point. The shallowly pitted interorbital space is slightly concave, and its width is about twice wider than the space between supratemporal fenestrae (STF). The frontal-parietal suture is concave anteriorly, and the suture does not enter the STF. The frontal-postorbital suture is zigzag shaped.

The skull table is much shorter than that of *Toyotamaphimeia machikanensis* (MOU F00001), but this is most likely due to the reconstruction error in MOU F00001 (discussed later). The anterolateral corners of the table at the level of the postorbitals are rounded, and the lateral sides are nearly straight and are widened posteriorly. Each supratemporal fenestra is wider than long, and its size is about the same as the orbit. In dorsal view, the posterior border of the STF is straight, and its anterior border is angled near the parietal-postorbital suture. The posterior bar of the STF is thinner than the lateral bar in dorsal view, as in derived gavialoids and in some tomistomines including *T. machikanensis* (MOU F00001). On the posterior wall of the fenestra, the upper half of the temporal canal is preserved.

Each postorbital forms the anterolateral region of the skull table. It is wider than long, and the outer margin above the descending process is rounded. The anterolaterally oriented descending process of the postorbital is inset from the skull table, and bears a prominent projection dorsally (Fig. 3). The postorbital bar is generally massive, anteroposteriorly thick, and oriented nearly horizontally. The upper half or the bar is triangular in section, whereas the bottom half is more

Fig. 2. KSNHM-F7-6 (Kishiwada specimen), A and B, skull in posterior view; C and E, skull in dorsal view; D, palatal maxillae in ventral view; F, tooth in mesial (distal) view. Stippled area indicates damaged bone. cnV, exit for cranial nerve V; cqo, cranio-quadrate opening; eoc, exoccipital; f, frontal; fae.q, quadrate foramen aëreum; j, jugal; lac, lacrimal; mx, maxilla; n, nasal; p, parietal; po, postorbital; perf, perforation; prf, prefrontal; ptf, postemporal fenestra; q, quadrate; qj, quadratojugal; soc, supraoccipital; sof, suborbital fenestra; sq, squamosal; vf, vagus foramen. Scale bars are 10 cm (A–E) and 2 cm (F).

dorsoventrally compressed.

In lateral view, each squamosal sends a wedged anterior process into the postorbital bar (Fig. 3). The groove for the external ear valve musculature is shallow and is flared anteriorly. Posteriorly, a significant squamosal prong extends posterolaterally.

The parietal merges with the squamosal and both contribute to a thin posterior margin of the STF, and the constricted medial border of STF (Fig. 2C and E). Its dorsal surface near the posterior margin is slightly concave and ornamented with large pits.

Each jugal sends a dorsoventrally thin ascending process, which borders the posterolateral corner of the orbit. The ascending process is inset from the main body of the jugal, separated by a deep gutter (Fig. 2C and E). Medially, the suture for the ectopterygoid extends up to the middle of the postorbital bar. The dorsal margin of the jugal lateral

to the postorbital bar is straight, while the ventral margin is concave (Fig. 3). Ventrally, just posterior to the suture of the ectopterygoid, a large depression (about 15.0 mm long axis: Fig. 4A) is present, and the bottom of the fossa is perforated as in *T. machikanensis* (MOU F00001). This perforation is interconnected with a large foramen on the dorsal surface of the jugal at the base of the postorbital bar. On the medial surface, a medial jugal foramen cannot be observed because this part is crushed.

The quadratojugals are incomplete and do not preserve the spina quadratojugalis, or the ascending process which would dorsally border the infratemporal fenestra. The posterolateral angle of the infratemporal fenestra is bordered by the quadratojugal-jugal suture, or quadratojugal alone. Ventrally, each quadratojugal bears a large foramen (about 5 mm diameter) near its posterior end (Fig. 4A).
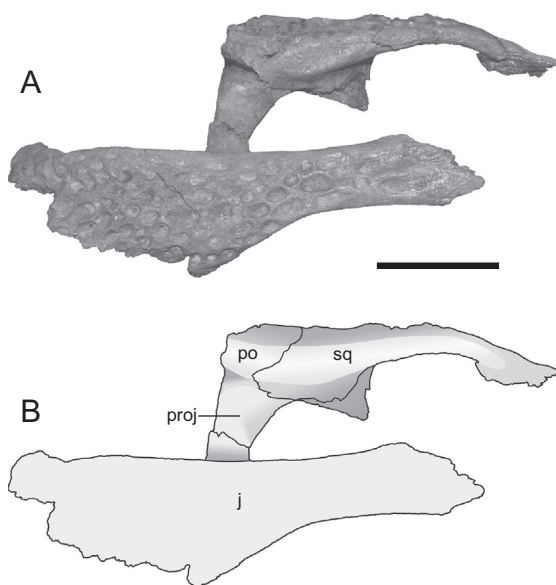
Fig. 3. KSNHM-F7-6 (Kishiwada specimen), posterior part of skull in left lateral view. j, jugal; po, postorbital; proj, projection; sq., squamosal. Scale bar is 5 cm.
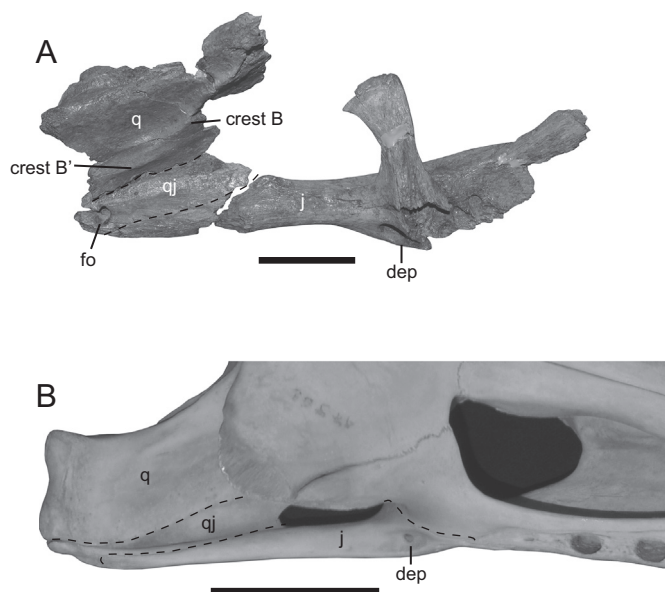

Fig. 4. Comparison of left jugal, quadratojugal, and quadrate in ventral view. A, KSNHM-F7-6 (Kishiwada specimen) and B, *Mecistops* cf. *cataphractus* (IRSNB 17962). dep, depression; fo, foramen; j, jugal; q, quadrate; qj, quadratojugal. Scale bars are 5 cm.

The dorsal surface of the quadrates is damaged, whereas their ventral surfaces preserve muscle scars (crest B and B′ in Iordansky, 1973: Fig. 4A). Posteriorly, the quadrate shows the lateral half of the cranio-quadrate opening (Fig. 2A and B). The quadrate foramen aëreum seems large, and opens at the dorsomedial corner of the medial hemicondyle.

In posterior view, the supraoccipital is triangular in shape, and much wider than deep (Fig. 2A and B). It is exposed on the posterior border of the skull table. The lateral posterior tuberosity is not prominent, and is not largely visible from a dorsal view. Lateral to the tuberosity, the postemporal fenestrae are damaged, but they appear to be tear drop shaped and widened laterally. The ventral portion of the right exoccipital shows the vagus foramen, which would be positioned lateral to the foramen magnum.

The only preserved tooth (Fig. 2F) is sharp and recurved. Its crown height and mesiodistal width at the base are 25.5 mm and 10.3 mm,

respectively, and the sectional shape is conical. There are two carinae on the opposed sides of the crown, and numerous striations run between them.

3.6. Mandible description

Fragments of the anterior portion of the mandible, and most of the posterior mandibular elements (dentary, surangular, angular, articular) are preserved (Fig. 5).

The anterior and middle portions of the left dentary preserve fourteen alveoli in total. Each alveolus projects anterodorsally, but the anterior alveoli are nearly horizontally oriented. In medial view, the level of alveoli ascends posteriorly, and the groove below the alveoli widens and deepens accordingly. Laterally, there are a series of foramina below the tooth row, and the foramina are larger posteriorly. In the posterior most part of the dentary, shallow grooves extend to the posterior dentary process between the bifurcated anterior processes of the surangular, and to the anterior corner of the external mandibular fenestra (Fig. 5A and B).

The symphyseal part of the left splenial is adjacent to at least four dentary alveoli (Fig. 5C and D). When its broken anterior and posterior extents are taken into account, it is most likely adjacent to five alveoli. In dorsal view, the splenial forms a slightly constricted V-shape as in *T. machikanensis* and *P. pani* (Kobayashi et al., 2006; Shan et al., 2009). Posterior to the symphysis, four alveoli are present, as inferred from a series of concavity on the lateral surface of the splenial.

The anterior processes of the surangular are unequal in length, and the dorsal one extends far anteriorly than the ventral one. The lateral surface of the surangular is flat posterior to the external mandibular fenestra. Posterior to it, the surangular forms a lateral wall of the glenoid fossa, which continues to its dorsal tip. Immediately lateral to the glenoid fossa is a series of vertically placed depressions. Medially, the surangular-articular suture is simple (articular does not have an anterior process) and the lingual foramen is entirely on the surangular (Fig. 5E and F).

The angular borders the external mandibular fenestra ventrally, and sutures with the ventral process of the dentary near the anterior end of the fenestra. The anterior process of the angular wedges between the dentary and splenial at the level of the last dentary alveolus.

The articular preserves a glenoid fossa with two depressions, in which the lateral one is larger than the medial one. The surangular-articular suture within the glenoid fossa is anteroposteriorly straight (Fig. 5C–D). The anterior surface of the articular is flat without the sulcus between the surangular-articular suture (Fig. 5E and F).

The external mandibular fenestra is long and narrow (Fig. 5A and B). The posterior process of the dentary intersects with the surangular anterior to the dorsal apex of the fenestra. The ventral margin of the fenestra is straight anteriorly and rounded posteriorly. The posterior corner of the fenestra is bordered by the surangular, and slightly ventral to it the surangular-angular suture intersects with the fenestra.

3.7. Taxonomic identification

The crocodylian from Kishiwada City, Osaka prefecture, Japan (hereafter the Kishiwada specimen) exhibits tooth size heterodonty, and 7th maxillary tooth anterior to the suborbital fenestra is largest, as in slender-snouted taxa including tomistomines (e.g., *Kentisuchus spenceri*, *Thecachampsa antiqua*, *Maomingosuchus petrolica*, *Penghusuchus pani*, and *Toyotamaphimeia machikanensis*: Owen, 1850; Kobayashi et al., 2006; Shan et al., 2009, 2017). The splenial symphysis of the Kishiwada specimen forms slightly constricted but relatively broad V-shape, which extends about 4–5 dentary tooth positions as in moderately long-irostrine gavialoids and tomistomines, including Taiwanese *P. pani* and Japanese *T. machikanensis* (Kobayashi et al., 2006; Shan et al., 2009). In an extant tomistomine *Tomistoma schlegelii*, the symphysis is more narrowly constricted. On the skull table, the posterior
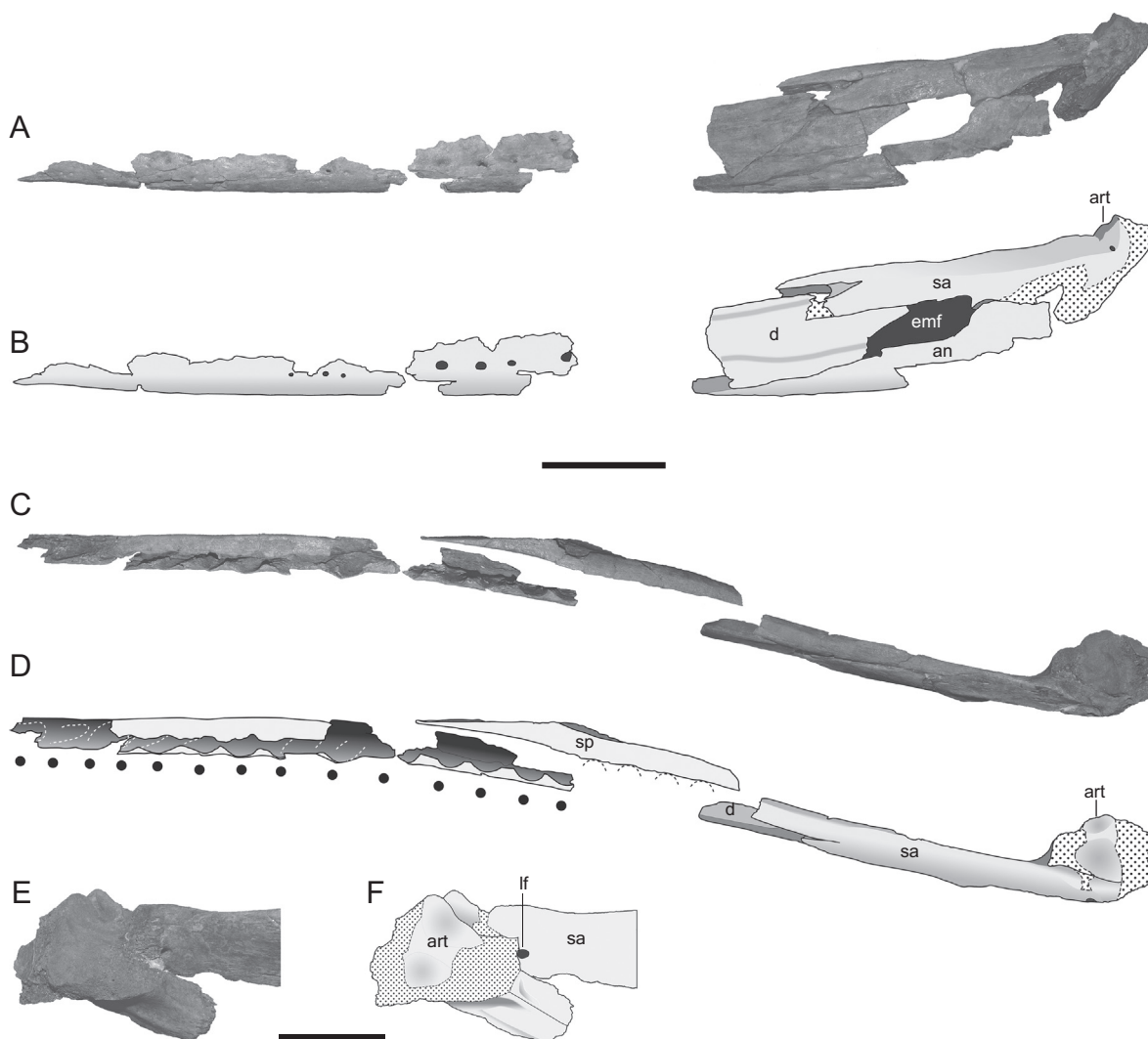
Fig. 5. KSNHM-F7-6 (Kishiwada specimen), left mandible in A and B, lateral views; C and D, dorsal views; E and F, posterior part in dorsomedial view. Alveolar positions are marked with filled circles. Stippled area indicates damaged bone. an, angular; art, articular; emf, external mandibular fenestra; d, dentary; lf, lingual foramen for articular artery and alveolar nerve; sa, surangular; sp., splenial. Scale bars are 10 cm (A–D) and 5 cm (E–F).

supratemporal bar of the Kishiwada specimen is thinner than the lateral bar, but is not extremely thin as in gavialoids, similar to some tomistomines (e.g., *Thecachampsa antiqua*, *Gavialosuchus eggenburgensis*, *Tomistoma lusitanica*, and *T. machikanensis*: Toula and Kail, 1885; Antunes, 1961; Myrick, 2001; Kobayashi et al., 2006). Posterior part of the skull table is damaged in *P. pani* (Shan et al., 2009). Along with the above characters, the Kishiwada specimen shares a unique character with the holotype of *T. machikanensis* (MOU F00001): deep and large depression with bottom perforations on the ventral part of the jugal at the base of postorbital bar (Fig. 4A). Our observation revealed that a similar character is also present in the extant crocodylian *Mecistops cataphractus* (both in West and Central African lineages proposed by Shirley et al., 2014: Fig. 4B) and *Crocodylus intermedius*. In these species, the ventral jugal depression is shallower than that in the holotype of *T. machikanensis* and the Kishiwada specimen, while the bottom perforation leads to a large internal room at the base of the postorbital bar, and this room is interconnected with the medial and dorsal jugal foramina. This character is unobservable in *P. pani* (Shan et al., 2009). In other crocodylians including *T. schlegelii*, a ventral jugal depression is not seen, yet there is a series of small perforations on the ventral jugal at the base of the postorbital bar, which may be interconnected with the dorsal and medial jugal foramina.

Among Asian tomistomines, Japanese materials (the Kishiwada specimen and the holotype of *T. machikanensis*) and Chinese and Taiwanese materials (*Maomingosuchus petrolica* and *Penghusuchus pani*) differ in the sutural pattern of the antorbital part. The degree of anterior extension of antorbital elements are frontal < prefrontal < jugal < lacrimal in Japanese materials (anterior tip of jugal missing in the Kishiwada specimen), consistent with an extant tomistomine *T. schlegelii*. On the other hand, the relationship is frontal < prefrontal = jugal = lacrimal in *P. pani* (Shan et al., 2009) and frontal = prefrontal = jugal < lacrimal in *M. petrolica* (Shan et al., 2017).

Since the original report by Taruno (1999), the taxonomic status of the Kishiwada specimen remained obscure until now. Taruno (1999) tentatively concluded that the Kishiwada specimen could be referred to as *T. machikanensis* based on the following similarities: narrow snout; orbit sub-circular in shape; orbit and supratemporal fenestra is subequal in size; short interorbital width; large supratemporal fenestrae. He also stated that both forms may also be similar in: nasals excluded from external naris; mandibular symphysis long, extending to the level of 13th and 14th tooth (alveolus); large 7th maxillary tooth. However, most of the characters he mentioned were symplesiomorphic and not diagnostic at lower taxonomic levels (Kobayashi et al., 2006). Only the large 7th maxillary tooth (alveolus) is diagnostic of the clade of *Penghusuchus pani* from the Miocene of Taiwan plus *T. machikanensis*
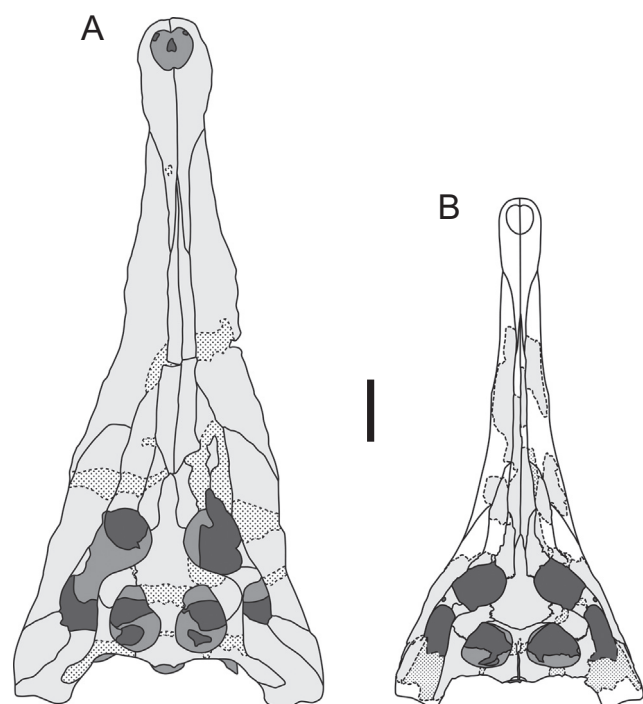
Fig. 6. Comparison of the skulls of A, MOU F00001 (holotype of *Toyotamaphimeia machikanensis*) (modified from Kobayashi et al., 2006) and B, KSNHM-F7-6 (Kishiwada specimen). Stippled area indicates damaged bone. Scale bar is 10 cm.

Fig. 7. Relationship of skull width and rostral proportion in *Tomistoma schlegelii*. AOW, width at anterior end of orbit; M5W, width at 5th maxillary alveolus; RL, rostral length (snout tip to anterior end of orbit). Star symbols are of the holotype of *Toyotamaphimeia machikanensis* (MOU F00001).

(Jouve et al., 2015), although the character state in the Kishiwada specimen is not confirmed from the preserved parts. Taruno (1999) also pointed out some differences between the two forms, which were additionally discussed in Kobayashi et al. (2006). They argued that the Kishiwada specimen has a slenderer snout and wider skull table compared to the holotype of *T. machikanensis*. Furthermore, the Kishiwada specimen's supratemporal fenestrae are wider than long, and frontal-parietal suture is concavo-convex, different from the holotype of *T. machikanensis* (Kobayashi et al., 2006) (Fig. 6).

Among these differences, slenderness of snout is not taxonomically informative because living tomistomine *Tomistoma schlegelii* develops more robust snout in the later growth stages (Müller, 1927; Iijima, 2017; Fig. 7 and Appendix 3). The large adults [BMNH 94.2.21.1 (skull length 839 mm, width 409 mm); USNM 211322 (skull length 783 mm, width 354 mm)] have wide and nearly triangular skulls as in the holotype of *T. machikanensis*. Since the skull of Kishiwada specimen is smaller than the holotype (skull width of the Kishiwada specimen is about 83% of that in the holotype of *T. machikanensis*), the difference in the snout slenderness is likely attributed to the different ontogenetic stages.

The remaining incongruence between the two specimens was probably brought when reconstructing the skull table of the holotype of *T. machikanensis*. The region in between the possible frontal-parietal suture and the interfenestral bar is filled with plaster in the holotype (Kobayashi et al., 2006; Fig. 6). Our observation of the holotype shows that the medial edge of the supratemporal fenestra (STF) is unnaturally angled, suggesting that the STF shape as well as the skull table would be much shorter. Accordingly, the frontal-parietal suture cannot be observed, and the state of this character is questionable.

An additional feature pointed by Furui et al. (2012) is a foramen on the ventral surface of the quadratojugal in the Kishiwada specimen (Fig. 4A). Observation on recent crocodylian species reveals that this character is widely present in Crocodylia including *Tomistoma*, and large adults have reasonably large foramina (BMNH 94.2.21.1; USNM 211322). Although the absence of such foramina in the holotype of *T. machikanensis* cannot be explained, this character is probably not
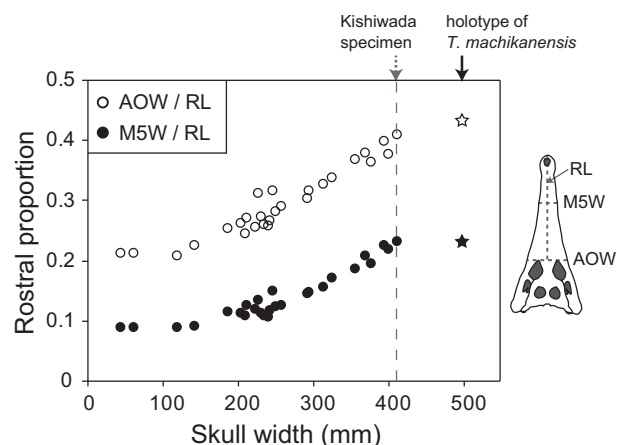
diagnostically important.

To confirm the phylogenetic position of the Kishiwada specimen (KSNHM-F7-6), a phylogenetic analysis was performed by adding the Kishiwada specimen into Jouve et al.'s (2015) taxon-character matrix. Although many skeletal elements are missing in the Kishiwada specimen, all codable characters are consistent with the holotype of *T. machikanensis*. The analysis recovered 232 equally parsimonious trees (tree length, 893; CI, 0.346; RI, 0.7). The Kishiwada specimen is deeply nested in the subfamily Tomistominae, and forms a sister-taxon relationship with the holotype of *T. machikanensis* (Fig. 8), supported by one unambiguous synapomorphy [character 47 (1): Angular-surangular suture passes broadly along ventral margin of external mandibular fenestra in the late ontogeny].

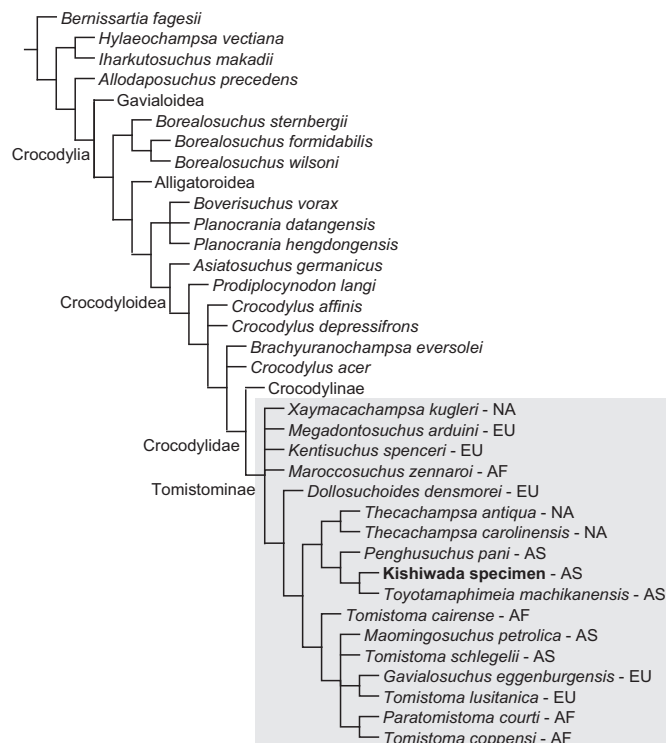In sum, (1) character comparison combined with a phylogenetic

Fig. 8. Strict consensus of 232 equally parsimonious trees (tree length, 893; CI, 0.346; RI, 0.7). AF, Africa; AS, Asia; EU, Europe, NA, North America.
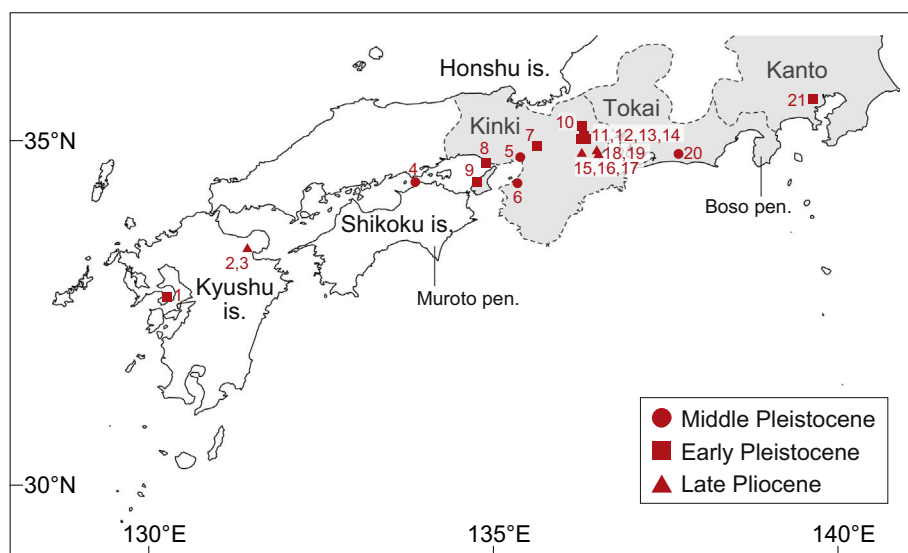
Fig. 9. Locality map of Japanese Pliocene-Pleistocene crocodylians. Number corresponds to Fig. 12 and Table 1. pen, peninsula.

analysis, (2) assessment of ontogenetic change in the skull shape using the modern relative *Tomistoma*, and (3) taking into account the reconstruction error in the holotype of *T. machikanensis* (MOU F00001) together warrant the taxonomic status of the Kishiwada specimen (KSNHM-F7-6) as *Toyotamaphimeia* cf. *machikanensis*.

4. Discussion: Pliocene-Pleistocene crocodylian record in Japan

4.1. Pliocene

Four localities in Honshu Island, and one locality in Kyushu island are known for Pliocene crocodylians (Fig. 9 and Table 1). Hattorigawa River floor in Iga City, Mie Prefecture yields numerous fragmentary elements including a right premaxilla, teeth, postcranial fragments, and trace fossils. The right premaxilla (Tanimoto and Okuyama, 1998; Fig. 10) is mediolaterally narrow, and its lateral margin is subparallel to the midline. The premaxillary tooth count is five as in *Toyotamaphimeia machikanensis* (Kobatake et al., 1965; Aoki, 1983; Kobayashi et al., 2006), in which 2nd to 5th alveoli are preserved. This narrow premaxilla, with several slender and recurved teeth from ~3.5 Ma of Iga (below Hattorigawa II tephra: Satoguchi and Nagahashi, 2012) suggest that a slender-snouted crocodylian, possibly a relative of *T. machikanensis*, was present in the Late Pliocene of Japan. Crocodylian materials from the similar age include the posterior portion of a skull, axial and limb fragments, and footprints from ~3.5 Ma of Suzukagawa River floor in Kameyama City, Mie Prefecture (Kobayashi, 2009; Okamura, 2009; Tanaka and Mikami, 2009; Tsumura, 2009; Nakagawa, 2014), teeth and osteoderms from 3.6–3.1 Ma of Isshinden-Kozubeta, Tsu City, Mie Prefecture (Mie Prefectural Museum, 2011; Hoshi, 2016), isolated teeth from ~2.7 Ma of Koka City, Shiga Prefecture (Matsuoka et al., 1991; Satoguchi and Nagahashi, 2012), and multitaxic bonebeds from ~3.0 Ma of Fukami River bank and floor, Ajimu, Usa City, Oita Prefecture (Aoki, 1983; Hoshizumi and Morishita, 1993; Hase et al., 2001; Satoguchi, 2001, 2008; Iijima et al., 2016). The last locality produced a number of sharp pointed teeth as well as *Alligator sinensis* materials, demonstrating the existence of a slender- and broad snouted crocodylians in the Late Pliocene of Kyushu.

4.2. Pleistocene

The Pleistocene crocodylian record is divided into early–mid Early Pleistocene (2.4–1.4 Ma) and late Early and Middle Pleistocene (1.2–0.3 Ma) (Figs. 8 and Table 1). The former includes teeth from

2.5–2.3 Ma of Goshiki Town, Hyogo Prefecture (above Kenjyogaoka II tephra: Nanko, 1996; Katoh et al., 2004) and isolated teeth from 2.1–1.9 Ma of four localities in Shiga Prefecture (below Narutani tephra, below Hara tephra, and around Kiryu I tephra: Isobe, 1990; Matsuoka et al., 1991; Takahashi, 1998; Yamamoto, 1998; Watanabe and Tanimoto, 2005; Abe, 2011). All of these teeth are slender and recurved. The other material is postcrania from ~1.4 Ma of Tama River floor, Kawasaki City, Kanagawa Prefecture (around Nishikubo tephra: Koizumi, 1995; Suzuki and Murata, 2011). This material is represented by a midline dorsal or pelvic osteoderm that is significantly wider than long without keel on its dorsal surface, being consistent with *T. machikanensis*.

The late Early and Middle Pleistocene crocodylians include several well dated materials from the Osaka Group of Osaka and Hyogo Prefectures, the oldest of which is an isolated vertebra from ~1.2 Ma of Yagi, Akashi City, Hyogo Prefecture (Byobugaura clay bed of the Osaka Group: Taruno, 1979). A bonebed material from ~1.1 Ma of Kaminokuchi, Takatsuki City, Osaka Prefecture (above Ma 1 bed of the Osaka Group: Kobayashi, 1977; Taruno, 1979) consists of a tooth, cervical to caudal vertebrae, ribs, and pelvic girdle elements (Fig. 11). The left iliac blade has a rounded dorsal margin without strong indentation, and there is a prominent anterior process, which is characteristic of *Bernissartia*, gavialoids, *Borealosuchus*, basal alligatoroids, and some "tomistomines," such as *Penghusuchus* and *Toyotamaphimeia* (Brochu, 1997; Kobayashi et al., 2006; Shan et al., 2009). Hence, this specimen might be a close relative of *T. machikanensis*. Two *Toyotamaphimeia* specimens from ~0.7 Ma of Nagareki-cho, Kishiwada City and ~0.5 Ma of Machikaneyama-cho, Toyonaka City, Osaka Prefecture (bottom of Ma 5 and below Ma 8 beds of the Osaka Group: Kobatake et al., 1965; Aoki, 1983; Taruno, 1999; Kobayashi et al., 2006; this study) are among the best preserved specimens of Japanese Plio-Pleistocene crocodylians. The youngest crocodylian record from Japan consists of more than a thousand skeletal fragments from ~0.4–0.3 Ma of the limestone fissure deposit in Inasa-cho, Hamamatsu City, Shizuoka Prefecture (below Yage tephra of the lower "Yage" Formation: Nojima, 2002; Nojima et al., 2014). Nojima (2002) suggested a close affinity of this specimen with extant *Tomistoma* based on the cranial and tooth morphology.

4.3. Japanese crocodylian survivorship in the Plio-Pleistocene climatic oscillations

Our review of Pliocene-Pleistocene records of Japanese crocodylians (Figs. 9 and 12, Table 1) reveals the continuous occurrence of

Table 1
The Plio–Pleistocene crocodylians from Japan.

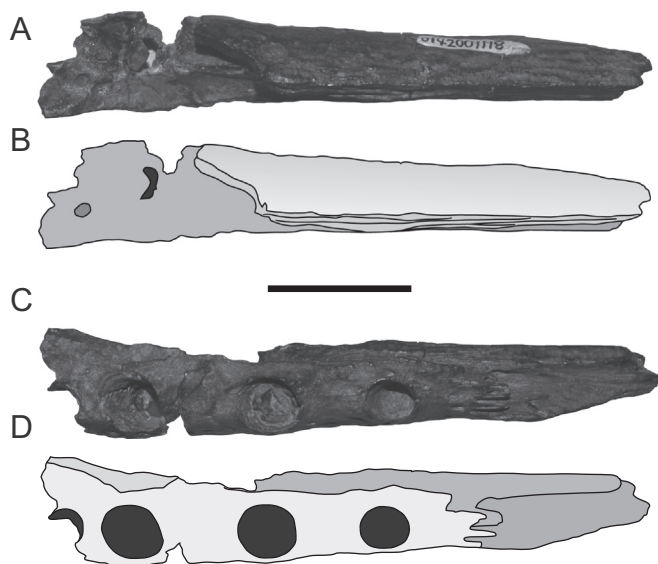| No.	Taxon	Age	Locality	Horizon	Element	Reference
1	Crocodylia indet.	Early Pleistocene	Kazusa-cho, Minamishimabara City, Nagasaki Prefecture	upper Kazusa Formation of Kuchinotsu Group	teeth and vertebrae	Otsuka, 1969
2	Alligator sinensis	Late Pliocene	Fukami River bank and floor in Ajimu-machi, Usa City, Oita Prefecture	middle Tsubusagawa Formation	partial skull, lower jaw, limbs, vertebrae, osteoderms, and teeth	Aoki, 2001; Iijima et al., 2016
3	Crocodylidae cf. Toyotamaphimeia	Late Pliocene	Ajimu-machi and Innai-machi, Usa City, Oita Prefecture	middle Tsubusagawa Formation	teeth	Aoki, 2001
4	Crocodylia indet.	Middle to Late Pleistocene	Bisan-Seto Sea, in Seto Inland Sea	Bisan-Seto Group	femur	Taruno, 1988
5	Toyotamaphimeia machikanensis	Middle Pleistocene	Machikaneyama-cho, Toyonaka City, Osaka Prefecture	below Ma8 Bed (Kasuri tephra), Ibaraki Formation of Osaka Group	a nearly complete skeleton	Kobatake et al., 1965; Kobatake and Kamei, 1966; Aoki, 1983; Kobayashi et al., 2006
6	Toyotamaphimeia cf. machikanensis	Middle Pleistocene	Nagareki-cho, Kishiwada City, Osaka Prefecture	near bottom of Ma5, Senpoku Formation of Osaka Group	partial skull, lower jaw, limbs, vertebrae, osteoderms, and tooth	Taruno, 1999; This study
7	Crocodylia indet.	Early Pleistocene	Kaminokuchi, Takatsuki City, Osaka Prefecture	above Ma1 Bed, lower Osaka Group	tooth, vertebrae, ribs, and pelvis	Kobayashi, 1977; Taruno, 1979
8	Crocodylia indet.	Early Pleistocene	Yagi, Akashi City, Hyogo Prefecture	Byobugaura Clay Bed (Ma0), lower Osaka Group	vertebra	Taruno, 1979
9	Crocodylia indet.	Early Pleistocene	Tsushi-saisaki, Goshiki Town, Hyogo Prefecture	above Kenjyogaoka II tephra, Atago Formation of Osaka Group	teeth	Nanko, 1996
10	Crocodylia indet.	Early Pleistocene	Taga Town, Inukami-gun, Shiga Prefecture	Shide tephra (correlated with Kiryu tephra I), Gamo Formation of Kobiwako Group	teeth	Tamura et al., 1993; Abe, 2011; Tanimoto and Iijima, 2017
11	Crocodylia indet.	Early Pleistocene	Shinden, Toriidaira, Hino Town, Gamo-gun, Shiga Prefecture	above Hara tephra, Gamo Formation of Kobiwako Group	teeth	Isobe, 1990; Takahashi, 1998
12	Crocodylia indet.	Early Pleistocene	Mikumo, Kosei-cho, Konan City, Shiga Prefecture	clay bed 80 m below Narutani tephra, Gamo Formation of Kobiwako Group	teeth	Watanabe and Tanimoto, 2005; Yamamoto, 1998
13	Crocodylia indet.	Early Pleistocene	Utta, Minakuchi-cho, Koka City, Shiga Prefecture	clay bed 150 m above Mushono tephra, Gamo Formation of Kobiwako Group	tooth	Watanabe and Tanimoto, 2005; Konishi 2015 personal communication
14	Crocodylia indet.	Late Pleistocene	Kibogaoka, Terasho, and Oki, Koka City, Shiga Prefecture	clay bed containing Sunasaka tephra, Koka Formation of Kobiwako Group	teeth	Matsuoka et al., 1991
15	Crocodylia indet.	mid Pliocene	Hattorigawa River floor in Hirata, Iga City, Mie Prefecture	below Hattorigawa II tephra, Ueno Formation of Kobiwako Group	footprint	Okuyama and Ochiai, 1993; Okuyama, 1994
16	Crocodylia indet.	mid Pliocene	Hattorigawa River floor in Hatamura and Kawara, Iga City, Mie Prefecture	between Hattorigawa I and II tephra, Ueno Formation of Kobiwako Group	teeth, pes, vertebrae, osteoderms, and coprolites	Okuyama, 1981, 1983, 1984, 1985, 1988; Kawaguchi and Kitada, 1982; Matsuoka et al., 1990; Matsuoka et al., 1991; Tanimoto and Kaede, 2000; Yamamoto, 1997
17	Crocodylidae indet.	mid Pliocene	Hattorigawa River floor in Hatamura, Iga City, Mie Prefecture	between Hattorigawa I and II tephra, Ueno Formation of Kobiwako Group	premaxilla	Tanimoto and Okuyama, 1998
18	Crocodylia indet.	mid Pliocene	Suzukagawa River floor in Nomura-cho, Kameyama City, Mie Prefecture	clay bed 150 m below Nomura tephra, Kameyama Formation of Tokai Group	posterior skull, vertebra, footprints	Kobayashi, 2009; Okamura, 2009; Nakagawa, 2014
19	Crocodylia indet.	mid Pliocene	Isshinden-kozubeta, Tsu City, Mie Prefecture	above Otani-ike tephra, Kameyama Formation of Tokai Group	teeth, osteoderms	Mie Prefectural Museum, 2011
20	Crocodylidae indet.	Middle Pleistocene	Yage, Inasa-cho, Hamamatsu City, Shizuoka Prefecture	lower 'Yage' Formation	skull, lower jaw, teeth, limbs, vertebrae, and osteoderms	Nojima, 2002; Nojima and Itoigawa, 2017; Nojima et al., 2007; Nojima et al., 2014
21	Crocodylia indet.	Early Pleistocene	Near Nikaryo Syukugawara, Tama Ward, Kawasaki City, Kanagawa Prefecture	above Nishikubo tephra, Iimuro Formation of Kazusa Group	vertebrae, libs, limbs, pelvis, and osteoderms	GMNH Koizumi collection; Koizumi, 1995

Fig. 10. A crocodylian right premaxilla (LBM 0142001118) from the mid Pliocene of Iga City, Mie Prefecture. A and B, dorsal views; C and D, ventral views. Scale bar is 2 cm.
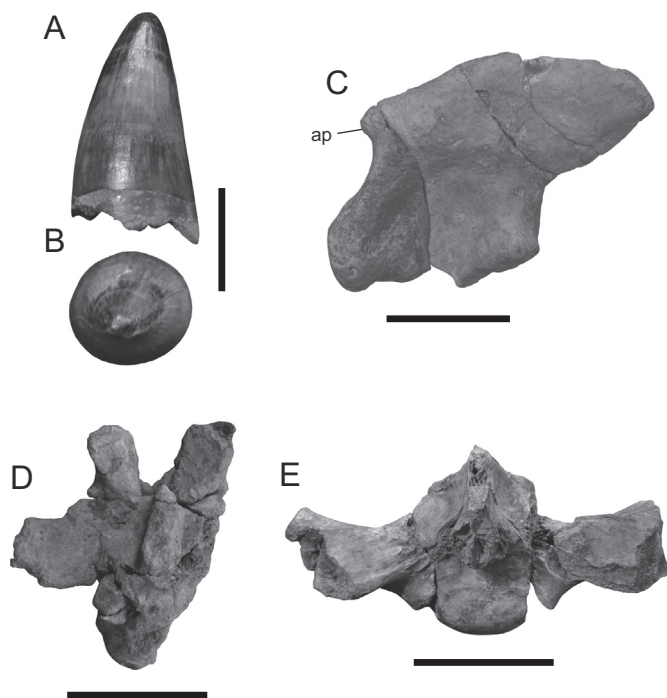

Fig. 11. Partial crocodylian skeleton from the Early Pleistocene of Takatsuki City, Osaka Prefecture. A and B, tooth crown (OMNH-QV 0278) in lingual (A) and apical (B) views; C, left ilium (OMNH-QV 0279) in lateral view; D, dorsal vertebra (OMNH-QV 0280) in dorsal view; E, second sacral vertebra (OMNH-QV 0281) in dorsal view. ap, anterior process of ilium. Scale bars are 1 cm (A and B) and 5 cm (C–E).

crocodylians in the Kinki, Tokai, and Kanto districts since the Pliocene until the late Middle Pleistocene. Those occurrences are chronologically well constrained by use of tephro- and magnetostratigraphy (Satoguchi and Nagahashi, 2012). Furthermore, the upper part of the Osaka Group was correlated with oxygen isotope stages (e.g., Masuda and Ito, 1999; Yoshikawa and Mitamura, 1999), by assigning marine clay beds into interglacial stages of the oxygen isotope curve (Lisiecki and Raymo, 2005). Ma0 and Ma1 marine clay beds, which yield the late Early Pleistocene crocodylians, are correlated with MIS 35 and MIS 31, respectively (Yoshikawa and Mitamura, 1999). Ma5 marine clay bed, from which the *Toyotamaphimeia* from Kishiwada was obtained, is
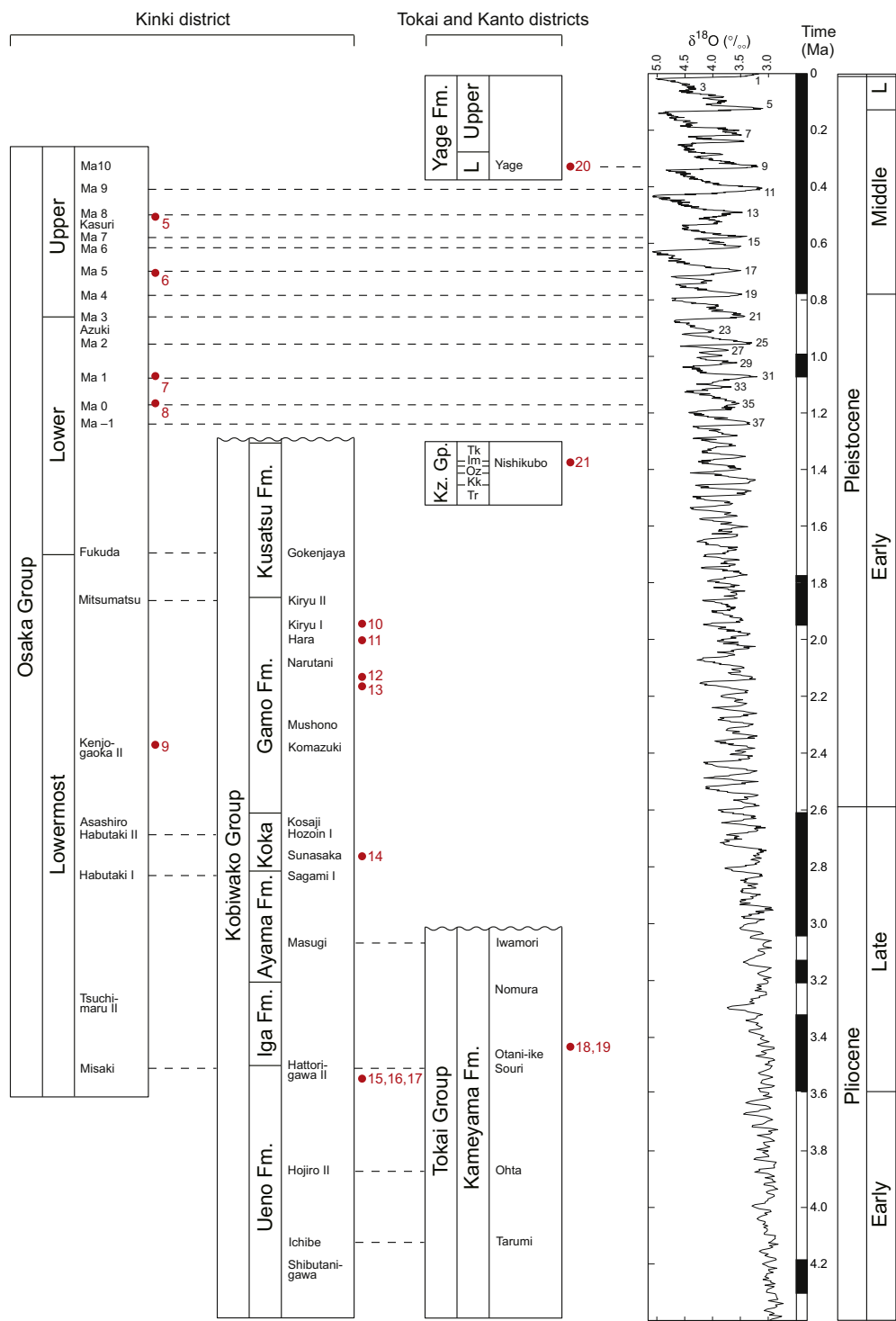
correlated with MIS 17 (Yoshikawa and Mitamura, 1999; Masuda and Ito, 1999). A sandy clay bed including the Kasuri tephra, from which another *Toyotamaphimeia* crocodylian occurred, is one meter below Ma8 marine clay bed that is assigned to MIS 13 (Yoshikawa and Mitamura, 1999). A potential *Toyotamaphimeia* record from the Shizuoka Prefecture (F3 bed of the lower "Yage" Formation) is correlated with MIS 9 (Nojima et al., 2014).

These crocodylian bearing horizons are situated in and/or near the marine clay beds in the Osaka Group, suggesting interglacial sea-level highstands. Even sediments associated with the Kasuri tephra below Ma8 marine clay bed were deposited under an interglacial condition because many thermophilous trees were found below the tephra bed (Ito et al., 2017). Thus, paleotemperature reconstruction of the corresponding interglacial stages is important for discussing the crocodylian survivorship during the Early to Middle Pleistocene of Japan. The temperature estimates (see 2.2. for methodology) of the crocodylian bearing beds in the lower and upper parts of the Osaka Group based on the thermophilous taxa are CMMT of 0.7–3.0 °C, MAT of 13.4–13.6 °C, and WMMT of 24.2–25.0 °C (Table 2). The alternative temperature estimates using the cold-loving taxa (CMMT: −1.5–1.8 °C; MAT: 9.8–12.2 °C; WMMT: 21.9–23.1 °C) should be interpreted carefully because such taxa could be transported from higher altitudes.

The previous analysis of recent crocodylian distribution indicated that temperature is the principal component limiting their distribution, although the presence of standing water is also important for their survival (Markwick, 1998a). According to his study, three temperature indices, (1) CMMT of at least 5.5 °C, (2) MAT of at least 14.2 °C, and (3) relatively lower mean annual range of temperature (Markwick, 1998a) together influence crocodylian distribution, thereby fossil crocodylians have been used as an climate proxy in the past (Markwick, 1994, 1998a, 1998b, 2007). However, living species' current distribution, which is the basis for the thermal limit estimation of crocodylians, differ slightly from the historical distribution during the last few centuries (Markwick, 1998a). For instance, the Chinese alligator *Alligator sinensis* showed much wider distribution before mid 19th through early 20th centuries along the lower reach of the Yangtze River (Wen et al., 1981). Recent climate data of China (IDBMC, 1984) suggests that the historical population of *A. sinensis* might tolerate increased seasonality and severe winter at some localities including Nanjing, Jiangsu (CMMT: 2.1 °C; MAT: 15.3 °C; WMMT: 27.9 °C), Hefei, Anhui (CMMT: 2.1 °C; MAT: 15.7 °C; WMMT: 28.3 °C), and Wuhu, Anhui (CMMT: 2.9 °C; MAT: 16.0 °C; WMMT: 28.7 °C). Thus, it is conceivable that crocodylians could cope with slightly more severe climate than previously perceived. Nonetheless, Japanese Pleistocene crocodylians in the Kinki district were supposed to be living near the lower thermal limit of crocodylians during the interglacial stages.

Climate deterioration during glacial stages, which became severer in the late Quaternary, would have impacted the crocodylian population in Japan. Paleotemperatures during a glacial stage in 1.9–1.8 Ma reconstructed from plant macrofossil assemblages in the Kobiwako Group in the central Kinki district were estimated as CMMT of −9 to −1.6 °C, MAT of 5.1–10.2 °C, and WMMT of 17.3–23.4 °C (Yamakawa et al., 2017). The subfreezing winter and low mean annual temperature prevented crocodylian survival in the central Kinki district during the glacial stages. They had most likely moved to the refugia along the Pacific coast and the exposed shelf along the Ryukyu islands, extending southwest from Kyushu.

The potential glacial refugia of crocodylians can be inferred based on the refugia position of plants whose thermal requirements are similar to crocodylians. *Elaeocarpus sylvestris* var. *ellipticus* (Elaeocarpaceae) and *Prunus zippeliana* (Rosaceae) are evergreen broadleaved trees with their northern distribution limits in the southern Boso Peninsula (Fig. 9), where the temperature condition is close to the crocodylian thermal limit (e.g., CMMT: 5.7 °C; MAT: 15.7 °C; WMMT: 26.7 °C in Chiba City, Chiba Prefecture) (JMA, 2002). Their refugia during the last glacial maximum was distributed along the Pacific coast

Fig. 12. Stratigraphic distribution of Plio-Pleistocene crocodylians from the Kinki, Tokai, and Kanto districts in Japan. Number corresponds to Fig. 9 and Table 1. The Plio-Pleistocene Series of these districts are time calibrated by tephro- and magnetostratigraphy (Satoguchi and Nagahashi, 2012) and oxygen isotope stratigraphy (Yoshikawa and Mitamura, 1999). The oxygen isotope record is adopted from Lisiecki and Raymo (2005). Im, Iimuro Formation; Kk, Kakio Formation; Oz, Ozenji Formation; Tk, Takatsu Formation; Tr, Tsurukawa Formation; Kz. Gp., Kazusa Group.

between the Muroto Peninsula and south Kyushu (Fig. 9), where rare haplotypes are found from the current local populations (Aoki et al., 2004). This molecular evidence might indicate the crocodylian survival in lowlands along the Pacific coast south of the Muroto Peninsula during the glacial stages.

After the end of each glacial period, crocodylians had perhaps re-expanded the distribution to the north, because their record in the central Honshu extends over multiple prominent isotopic glacial peaks

(MIS 12 and 16) in the Middle Pleistocene (Fig. 12). Long term monitoring surveys on once depleted populations of the saltwater crocodiles demonstrated that there was a rapid increase in the population density after the hunting stopped (Webb et al., 2000; Fukuda et al., 2011). This strong recovery, with the ability of long distance travel in both freshwater and estuarine habitats (Campos et al., 2006; Read et al., 2007; Lance et al., 2011) could help the multiple range re-expansion over the Plio-Pleistocene.

Table 2
Paleotemperature estimates using the thermophilous and cold-loving taxa in the plant macrofossil assemblages from Ma0, Ma1, Ma5, and Ma8 marine clay beds in the Osaka Group. Abbreviations: J, Japan; Ch, China; CMMT, coldest-month mean temperature; MAT, mean annual temperature; WMMT, warmest-month mean temperature. Temperature values in bold letters were accepted and those in italics were rejected.

Taxon	Locality of distribution limit				Temperature (°C)			Reference	Occurrence in the Osaka Group
	Locality	Altitude (m)	Latitude N	Longitude E	CMMT	MAT	WMMT		
Thermophilous taxon									
Ficus pumila	Tsukushino, S. Fukuoka, J.	350	33°31′	130°34′	**3.0**	**13.4**	**24.2**	Tsutsui, 1992	Ma0, Ma8
Syzygium buxifolium	Mt. Huang, S. Anhui, Ch.	750	30°05′	118°10′	**1.5**	**13.4**	**24.3**	Hu and Liang, 1996	Ma8
Paliurus hemsleyanus	Sennojia, W. Hubei, Ch.	950	31°45′	110°45′	**0.7**	*14.5*	**25.0**	Zhu and Song, 1999	Ma0, Ma1, Ma5, Ma8
	Mt.Tianmu, Zhejiang, Ch.	550	30°20′	129°26′	*1.6*	**13.6**	*25.5*	Ding et al., 2009	
Cold-loving taxon									
Thuja standishii	Sasazu, Toyama, J.	550	36°29′	137°17′	**-1.5**	**9.8**	**22.8**	Takahashi, 1962	Ma0
Picea polita	Igawa, C. Shizuoka, J.	750	35°11′	138°12′	**0.6**	**11.1**	**21.9**	Hayashi, 1952	Ma1, Ma5
Fagus japonica	Igawa, C. Shizuoka, J.	550	35°10′	138°11′	**1.8**	**12.2**	**23.1**	Takahashi, 1962	Ma8

It is also possible that crocodylians had died out from Japan during glacial periods, but they had migrated from the Asian continent through a land bridge or by coasting when the climate was moderate. Stratigraphic distribution of warm-water diatoms, foraminifers, and mollusks in the Plio-Pleistocene deposits along the coast of the Japan Sea suggests that the southern channel of the Japan Sea was periodically opened for few interglacial intervals during 3.5–1.7 Ma, but for almost all interglacial intervals after 1.7 Ma (Kitamura et al., 2001; Kitamura and Kimoto, 2006). Hence, crocodylians might have been able to disperse from the mainland Asia into Japan across the land bridge until 1.7 Ma. Even without the formation of a land bridge, they would migrate across ocean via fluvial capture on the shallow shelf, as proposed for the *Gavialis* dispersal from the mainland Asia into Java in the Pleistocene (Martin et al., 2012). In support of this view, relative abundance data of a warm-water planktonic foraminifera through time suggested that the Tsushima Current, which passes the southern channel of Japan through the Japan Sea, was much lower in salinity during interglacial periods until 1.7 Ma (Kitamura and Kimoto, 2006), probably due to the freshwater delivered from the eastwardly extended Chinese mainland (Nakamura et al., 1999).

Because of the constantly opened southern channel of the Japan Sea, and increased volume and higher salinity of the Tsushima Current during interglacial highstands after 1.7 Ma (Kitamura and Kimoto, 2006), crocodylian migrations between the Asian continent and Japan became restricted by means of transoceanic travels in saline water. Among Japanese crocodylians, a tomistomine *Toyotamaphimeia* might have salt tolerance because many of the fossil tomistomines have been recovered from estuarine and coastal settings (e.g., Brochu, 2003; Piras et al., 2007; Jouve et al., 2015), although the living relative *Tomistoma* is restricted to freshwater. On the other hand, the Pliocene *Alligator sinensis* from Japan (Iijima et al., 2016) most likely lacked lingual salt gland as in extant *Alligator* (Taplin and Grigg, 1989). This prevented Japanese *A. sinensis* from migrating across ocean after severe glacial periods, although short offshore travels could be possible, as rarely reported in extant alligatorids (Elsey, 2005; Grigg and Kirshner, 2015). In the future, stable isotope analyses on fossil teeth, as implemented in previous works (Wheatley, 2010; Martin et al., 2015; Whiting et al., 2016) will be helpful to discuss the physiology and dispersal potential of Japanese crocodylians.

During the Plio-Pleistocene, both of two Japanese crocodylian lineages (*Toyotamaphimeia* and *Alligator*) had wider distributions in the East Asia across the East China Sea. Fossil crocodylians showing affinity with East Asian tomistomines (large 7th maxillary tooth: synapomorphy of *Toyotamaphimeia* + *Penghusuchus*) were found in the Plio-Pleistocene of Taiwan (Takekawa et al., 2017) and the Holocene of Guangdong Province in China (Zhao et al., 1986). Similarly, definite and potential *A. sinensis* fossils were recovered from the Pleistocene of Taiwan (Shan et al., 2013), Guangdong Province in China (Huang et al., 1988), and Late Miocene-Pleistocene of Thailand (Claude et al., 2011).

Geographical ranges of these two East Asian crocodylian lineages were largely contracted by the climate deterioration during the Plio-Pleistocene and anthropogenic effects after the rise of humans, leaving only *A. sinensis* in Anhui Province, China at present (Zhao et al., 1986; Thorbjarnarson and Wang, 2010). Comparable range contraction of crocodylians occurred globally in the Plio-Pleistocene, and crocodylians were progressively restricted to major river systems and coastal plains in lower latitudes toward the Recent (Markwick, 1994, 1998a, 1998b, 2007).

5. Conclusions

A description of a crocodylian material from the Middle Pleistocene of Japan, and compilation of the fossil record of Japanese Pliocene-Pleistocene crocodylians show that crocodylians including a tomistomine *Toyotamaphimeia* had continuously existed from ~3.5 Ma in the Pliocene through ~0.3 Ma in the Pleistocene in Japan. Paleotemperature estimates of the crocodylian-bearing interglacial beds suggest that Japanese Pleistocene crocodylians were living near their perceived lower thermal limit. During glacial periods, they might have survived in the southern refugia, or became locally extinct from Japan. The strong population recovery, combined with potential dispersals from the mainland Asia across land bridges and through oceans could explain the continuity of the Japanese crocodylian record during the Pliocene-Pleistocene. However, repeated range contractions in the glacial periods might have reduced the genetic diversity of crocodylians, leading to their final demise in Japan.

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